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Wood taphonomy in a tropical marine carbonate environment: Experimental results from Lee Stocking Island, Bahamas

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ABSTRACT

Both teredinid bivales and limnorid isopods attacked wood that was deployed experimentally for two years in a carbonate environment. On average, wood samples collected after one year on the sea floor lost 17% of their original surface area to *Limnoria* and 50% of their original volume to teredinids. After two years on the sea floor, wood samples lost an average of 39% of their original surface and 74% of their original volume. All samples of kiln-dried lumber (*Pinus*, *Sequoia*, *Araucaria*, *Magnolia*, and *Quercus*) experienced significantly more attack by teredinids and *Limnoria* than samples of *Quercus stellata* (post oak) branch wood that experienced terrestrial decomposition in a warm-temperate environment for five years before deployment on the sea floor. Taphonomic loss rates for wood in marine environments based on kiln-dried lumber may overestimate loss rates for natural wood entering marine environments after initial decomposition in terrestrial environments. Burial appears to play an important role in wood taphonomy. Burial to a depth of >3 cm inhibited destruction by *Limnoria*, but not teredinids, possibly due to the greater tolerance of molluscs for low O_2 levels and the ability of teredinids to raise their siphons above the wood surface. Both limnorids and teredinids may contribute to the formation of *Teredolites* (disaggregated, sediment-filled teredinid borings). Limnorid isopods remove the surface of wood exposing the calcite-lined borings of teredinids. Once their calcite-lined borings are exposed, teredinid are susceptible to predation, and in the aftermath of predation, teredinid borings may become sediment filled. Exposure also causes the calcite-lined borings to break and disaggregate, leading to the formation of *Teredolites*. The fossil record of teredinids reaches back to the Jurassic. *Limnoria* traces in the surface of wood are distinctive and diagnostic at the species level; however *Limnoria* have a sparse fossil record.

1. Introduction

Wood is common in modern and ancient marine sediments. Permineralized wood appears in marine environments beginning in the Middle Devonian and occurs frequently in Late Devonian black shales (Campbell, 1963; Arnold, 1970; Chitaley and Cai, 2001; Meyer-Berthaud et al., 2004 and references therein). In both ancient and modern marine sediments, two ubiquitous types of marine palynodebris (small, sedimentary organic particles that range in size from 10 μm to 250 μm), brown wood and black debris, derive from wood; and wood is a signficant source of a third type, palynowafers (Oboh, 1992; Boulter, 1994). Larger pieces of wood also occur in modern ocean sediments. Approximately 24% of the stations occupied in the 1950–1952 Galathea Cruise to collect sediments and organisms from the sea floor between 20°N and 50°S in the Atlantic, Indian and Pacific Oceans yielded wood (Bruun, 1959; Knudsen, 1961). Wolff (1979) reported abundant wood fragments in deep-sea sediments from the Puerto Rico and Caymen Trenches. Pailleret et al. (2007) found wood on the sea floor at depths of 560–580 m in the Vanatua Archipelago. In the Gulf of Mexico, Traverse (1994) found wood fragments in fine-grained sediment samples collected over 5 miles from the coast. The widespread distribution of marine wood communities, wood-eating invertebrates and their predators, reflects the availability of wood in marine environments (Knudsen, 1961; Turner, 1973, 1977; Wolff, 1979; Pailleret et al., 2007; Voight, 2007, 2008).

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Bromley et al. (1984) defined wood grounds as exhumed, xylic (i.e. woody) peats inundated by marine water and colonized by boring organisms. The largest boring organisms to colonize wood, and the most likely to appear in the stratigraphic record, are pholad and teredinid molluscs, which leave clavate or club-shaped borings that may or may not be lined with calcite. Kelly and Bromley (1984) named these clavate borings *Teredolites*. Savrda et al. (1993) recognized that exhumed, xylic peat is relatively rare in the fossil record. Accordingly, they broadened the definition of wood ground to include: 1, log grounds, defined as isolated logs on a bedding plane; 2, relict log grounds, defined as *Teredolites* in life position with little or no fossil wood in between the borings; 3, ghost log grounds, defined as disassociated *Teredolites* at or near the site of the now decayed wood substrate; and 4, lag layers consisting of reworked *Teredolites* (Savrda et al., 1993). In marine ecosystems with molluscan and arthropod wood borers, reworked *Teredolites* may be the only remnant of former log grounds (Savrda et al., 1993).

The earliest widespread log-grounds are Late Devonian marine shales with permineralized wood (Arnold, 1970; Chitaley and Cai, 2001; Meyer-Berthaud et al., 2004). Permineralized log grounds appear to be less common after the Late Devonian; however, permineralized wood occurs in Late Paleozoic, Mesozoic and Cenozoic marine deposits (Pennyslvanian—Scott et al., 1997; Permian—Mack et al., 2003; Jurassic—Garcia et al., 1998; Cretaceous—Chan, 1992; Wilson and Taylor, 2001; Paleocene—Donovan et al., 2009; Eocene—Pirrie et al., 1998; Savrda et al., 2005).

Teredolites, the most common trace fossil associated with wood, occurs from the Jurassic to the Recent (Bromley et al., 1984; Kelly and Bromley, 1984; Kelley, 1988 and references therein; Chan, 1992; Pemberton et al., 1992; Hettinger et al., 1993; Savrda et al., 1993; Gale, 1995; Huggett et al., 2000; Taylor and Wilson, 2003; Gingras et al., 2004; Kiel and Goedert, 2006; Vahldiek and Schweigert, 2007). Savrda and co-workers made detailed observations of log-ground diagenesis and described the depositional settings that lead to their preservation in marine sediments (Savrda et al., 1993, 2005). Gingras et al. (2004) investigated the taphonomy of modern log grounds in intertidal settings. However, the taphonomic processes that lead to the fossilization of wood in marine environments, and to the production of *Teredolites* beds have not been studied experimentally.

Much of the work on wood in marine ecosystems has focused on the destruction of shallow pier pilings (Miller, 1924; Hill and Kofoid, 1927; Edmondson, 1955; Singh and Sasekumar, 1996 and references therein), and the role of bacteria in the decomposition of particulate lignin (Benner et al., 1984, 1986a,b). Turner deployed wood panels in deep water off Woods Hole, Massachusetts (1830 and 3506 mbsl), Florida (100 mbsl), Port Hueme, California (2400 mbsl) and the Bahamas (1726 and 2066 mbsl; Turner, 1966, 1973, 1977). Only the Port Hueme, California study resulted in a published report describing the damage done to wood samples by marine invertebrates (Muraoka, 1962, 1964, 1965, 1966a,b,c, 1967). Voight (2007) deployed wood panels at depths of 1550–3232 m in basalt, basalt talus and sediment in the Northeast Pacific, off the coast of Washington State in order to investigate the diversity of wood-eating (xylophagid) molluscs. However this study did not address the rate of wood destruction by xylophagids.

Marine molluscs (teredinids and pholads) and arthropods belonging to the Isopoda (*Limnoria*) macerate wood in modern marine habitats (Menzies, 1959; Turner and Johnson, 1971; and Turner, 1973, 1977). Sipunculids have been found inhabiting wood and may macerate it as well (Rice, 1985). Gingras et al. (2004) identified spionid polychaetes as wood boreres in the intertidal zone of Willapa Bay, Washington State; however it is not clear whether these organisms macerate wood. Maceration, which increases the surface area of wood available for microbial attack, facilitates bacterial and fungal decomposition in terrestrial and marine ecosystems (Mann, 1975; Swift et al., 1979). Many studies have focused on the biology of the teredinids and pholads, including their nutrition and reproductive patterns at shallow depths (Nair and Saraswathy, 1971 and references therein; McGinnes et al., 1976; Distel and Roberts, 1997; Morton, 1978; Hoagland, 1986).

Several factors may contribute to wood preservation in marine environments. Taphonomic studies of marine invertebrate shells indicated that burial below the taphonomically active zone leads to preservation (Davies et al., 1989; Olszewski, 2004). Studies of wooden pier pilings suggested that certain woods resist marine boring organisms due to their anatomy and biochemistry: both high silica and high tannin content impeded attack of pier pilings in San Francisco Bay (Hill and Kofoid, 1927; Edmondson, 1955; Nair and Saraswathy, 1971; Southwell and Bultman, 1971). However, these studies did not address the role of burial in wood preservation.

Except for the introduction of vessel elements, found in angiosperm and gnetalean wood begining in the Cretaceous (Taylor and Taylor, 1993), the basic anatomy and morphology of wood have not changed significantly since the Late Devonian. Thus, knowing the taphonomy of wood in modern marine environments will help us to understand the taphonomic processes affecting wood in marine environments through the Phanerozoic. To investigate the processes and rate of wood destruction in marine environments, we deployed six types of wood in a carbonate shelf environment (Lee Stocking Island, Great Exuma, Bahamas) at depths ranging from 15 to 267 meters below sea level (mbsl; Figs. 1 and 2). We deployed both conifer and angiosperm wood in order to test whether differences in anatomy and wood biochemistry related to the evolution of angiosperms in the Late Mesozoic have affected the taphonomy of wood in marine environments (Rayner and Boddy, 1988; Taylor and Taylor, 1993). This study is part of the Shelf and Slope Experimental Taphonomy Initiative (SSETI) designed to determine taphonomic signatures and study taphonomic rates on the Bahamas Banks and in the Gulf of Mexico over a period of one to twenty years (Powell, this issue). Full details of the SSETI program and experimental results for shells, crabs and echinoderms appear in Parsons et al. (1997), Parsons-Hubbard et al. (1999), Parsons-Hubbard et al. (2008); Callender et al. (2002), Powell et al. (2002), Powell et al. (2008), Staff et al. (2002); Walker et al. (2002). This contribution focuses on the destruction of wood deployed in a carbonate environment by arthropods and molluscs after two years on the sea floor.

2. Methods

2.1. Site description

At Lee Stocking Island, Great Exuma Chain, Bahamas, samples were deployed along the AA and BA transects established by the Perry Institute for Marine Science Caribbean Marine Research Center and the National Undersea Research Program using SCUBA and a submersible (the *Nekton Gamma*). Transect AA lies directly off an inlet separating Lee Stocking Island from Adderly Cay (Fig. 1). Transect BA lies parallel to, and southeast of, Transect AA. Four replicate sample arrays were deployed at each of 21 total sites (Table 1, Fig. 2). The sites lie at a range of depths (15–267 mbsl) and include the following substrates and environments of deposition: 1, sand channels and a hard ground on the top of a carbonate platform (15 mbsl in Table 1 and on Fig. 2); 2, sand channels at the edge of the platform (30 mbsl in Table 1 and on Fig. 2); 3, hardground ledges on the platform wall (from 70 to 88 mbsl in Table 1 and on Fig. 2); 4, fine-grained carbonate sand of the upper and lower talus slope (repectively, 183 mbsl and 210–226 mbsl in Table 1 and on Fig. 2); and 5, the crest and trough of relict submarine carbonate sand dunes (253–267 mbsl in Table 1 and on Fig. 2). Most of the experiments remained in place over the two years of this study. However storm activity moved experiments from site AA50RID from the ridge to the channel, Storm activity also moved experiments at sites AA100SI and